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NESTING BEHAVIOR OF *KROMBEINICTUS NORDENAE* LECLERCQ, A SPHECID WASP WITH VEGETARIAN LARVAE (HYMENOPTERA: SPHECIDAE: CRABRONINAE)

KARL V. KROMBEIN AND BETH B. NORDEN

Department of Entomology, National Museum of Natural History, Smithsonian Institution, MRC 165, Washington, DC 20560, U.S.A.

Abstract.—Nesting behavior of the recently described Sri Lankan wasp, *Krombeinictus nordenae* Leclercq, is discussed. Females nest in the hollow internodes of the leguminous myrmecophyte, *Humboldtia laurifolia* Vahl. The biology of this stem-nesting crabronine is unique among Sphecidae in several aspects. An adult female exhibits remarkable maternal care, rearing one larva at a time, and feeding it progressively. Progressive provisioning has not been noted previously for any Crabroninae. Nests lack cell partitions and mature larvae are transported to the basal regions of their stems for cocoon spinning. The cocoon is also unlike that of any other known crabronine species, exhibiting adaptations to internode morphology and allowing movement of adults within the nest cavity. Finally, *K. nordenae* is remarkably different from all other known Sphecidae in feeding pollen rather than paralyzed arthropod prey to its larvae.

Key Words: Sphecidae, Crabroninae, *Humboldtia*, Sri Lanka, internode, myrmecophyte, cocoon, pollen

Sri Lanka has been called the land of serendipity. A recent example is the amazing nesting behavior of a Ceylonese wasp, a newly described genus and species, *Krombeinictus nordenae* Leclercq (1996). This pretty little wasp (Fig. 1), 5–6 mm long, has creamy to pale yellow markings on its black head and thorax, and a mostly light red abdomen bearing narrow, transverse, brown to black stripes on some of the dorsal segments. *Krombeinictus* belongs to the Sphecidae, normally a family of predaceous, mostly solitary wasps.

MATERIALS AND METHODS

Our first encounter with this species was when we received a single male of *K. nordenae* from a colleague, Prof. Fred R. Rickson. It was among a few wasps that emerged from a dozen internodes of the myrmecophyte, *Humboldtia laurifolia* Vahl, that he collected in the Sinharaja Forest Reserve in Sri Lanka in 1992.

We visited Sri Lanka in 1993, and spent five days (18–20 Jul and 2–3 Aug) in the rainforest near Gilimale, Ratnapura District, 06°46′N, 80°26′E. We hoped to make behavioral observations on *Krombeinictus* during this brief period, but intermittent rains of the delayed monsoon season precluded nesting activity by the wasps. However, we censused about a thousand internodes from *H. laurifolia*, and placed several hundred unopened stems directly into alcohol for subsequent study. These internodes were split open carefully in the laboratory to avoid damaging associated organisms, and notes were made on their contents.

Figs. 1–2. *Krombeinictus nordenae*, female. 1, Lateral view. 2, Frontal view of head.

Humboldtia laurifolia Vahl
(Figs. 3–6, 12–15)

This botanical section is condensed from a detailed account of the plant's morphology in Krombein et al. (in prep.). *Humboldtia laurifolia* (Fabaceae) (Fig. 3) occurs only in Sri Lanka; three other species of the genus and one variety occur in southern India. *Humboldtia laurifolia* is a small understory tree, growing to a height of about 10 m, found in the lowland rainforest of the southwestern quadrant of Sri Lanka. It usually grows along streams or in seeps, is highly gregarious, and occurs in groups of ten to several hundred trees.

Humboldtia laurifolia and two of its Indian congeners, *H. brunonis* Wallich and *H. decurrens* Beddome ex Oliver, are of particular interest to naturalists because they are myrmecophytes that have coevolved with several species of ants. The trees provide swollen internodes, each with a self-opening entrance, that serve as domatia for the ants. The trees also provide an abundance of extrafloral nectaries on leaves, stipules and inflorescences whose secretions are attractive to the ants. In turn, the ants protect the foliage, especially the tender, young leaves, from herbivory.

Humboldtia laurifolia is typical of legumes in having pinnately compound leaves, each leaf having four to six pairs of opposite leaflets (Fig. 4). As in many legumes there is a developmental period during which a flush of four or five new internodes, each with an associated leaf, is produced over a period of two months. As the internode develops, the apical part becomes inflated, and is filled with pith. When the internode matures, the pith collapses against the inner wall, forming a hollow cavity, and a slit-like opening develops near the apex (Fig. 5). The opening widens gradually until ants or other small organisms can access the hollow domatium. Some occupants apparently gnaw at the more or less elliptical opening, transforming it to an oval or circular opening that is gradually rimmed by a callus (Fig. 6), the plant's response to the injury. Aculeate Hymenoptera (ants, wasps, bees) remove the pith to make the cavity larger, except for one species of solitary crabronine wasp, *Crossocerus mukalanae* Leclercq which uses the pith in constructing its nest in the cavity.

We found aculeates nesting in internodes ranging in length from 4.3 to 11.2 cm. The basal end of the internode is woody to a variable extent, so the length of the cavity varies from 3.2–6.3 cm. The woody outer wall of the internode is 0.3–0.7 mm thick. The internode entrances are elliptical to circular in shape with width to length measurements ranging from a minimum of 1.1 × 1.1 mm to a maximum of 1.2 × 1.8 mm.

Figs. 3–6. *Humboldtia laurifolia*. 3, Habitat; collecting on plant. 4, Leaf; note swollen internode at lower right. 5, Internode opening early in development. 6, Internode opening to *Krombeinictus nordenae* nest; note callus around hole.

Krombeinictus nordenae Leclercq
(Figs. 1, 2, 7–11)

Apparently an uncommon wasp, we found only eight specimens (6 ♀, 2 ♂) in *Humboldtia* internodes at Gilimale as compared to several hundred of its fellow crabronine, *Crossocerus mukalanae*. It has unusual morphology in that it is the only genus of Crabroninae, other than the Oriental *Vechtia* Pate, in which both sexes possess a triangular lamella overhanging the deep scapal basin (Fig. 2).

The female is unusual morphologically in the Crabroninae in lacking a pygidium delimited by carinae on the last abdominal tergum. Instead there is a median brush of several rows of close-set, erect setae (Fig. 7). The last abdominal segment of females usually bears the residue of a secretion from abdominal glands (Fig. 8) that we believe may function as an ant guard. We suspect that a nesting female uses its brush of setae to smear this secretion around the nest entrance to deter predators and parasites from entering while the adult wasp is foraging.

The Oriental *Piyumoides* Leclercq, considered by him (1996) to be the genus most closely related to *Krombeinictus*, also lacks a pygidium. Females, however, lack the median brush of setae on the last abdominal tergum. There is no secretion from abdominal glands on this segment in females of three of the four known species in our collection.

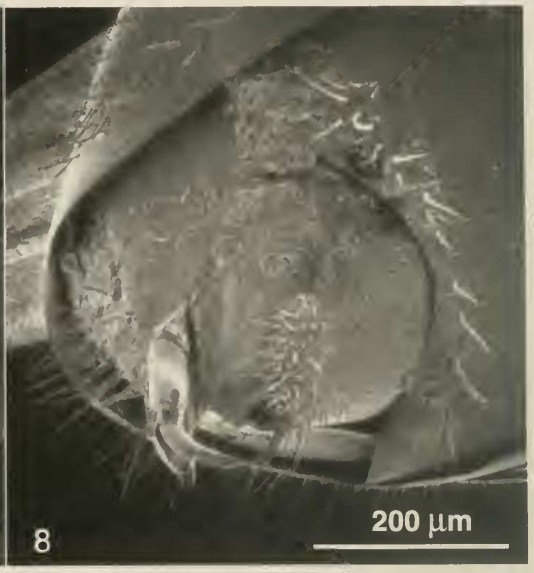
Nest.—We found only ten nests of *K. nordenae* compared with about 75 of *C. mukalanae*, and adult females were present in only four of them. We believe that the missing females took flight during the period between gathering *Humboldtia* branches, and placing the internodes in alcohol. Several females were found sheltering in empty internodes.

One typical nest exhibited the sequence of nesting activity (Fig. 9). The internode was 6.3 cm long, and the maximum width was 4.0 mm. The interior cavity was 5.0 cm long and had a maximum width of 3.4 mm. When we split the internode, we found a small wasp larva, 2 mm long, on the wall of the cavity just below the entrance hole. The female was lower in the cavity, probably a reaction to being immersed in alcohol when the internode was preserved. There was a wasp pupa with well developed adult coloration in its cocoon at the bottom of the cavity. Ten mm above this cocoon was a second cocoon that contained a post-defecated larva just prior to pupation.

From these data, and observations in other internodes with nesting *K. nordenae*, we deduce the following behavioral sequence. The foundress lays the first egg on the inner cavity wall just below the entrance. When the larva hatches, she feeds it progressively until mature. The wasp then transports it to the bottom of the cavity where it subsequently spins its cocoon, pupates, and slowly begins to develop adult coloration. After the wasp takes the mature larva below, she lays a second egg just below the entrance. That larva is fed progressively, and, when mature, it is transported lower in the cavity for cocoon spinning. The same cycle is repeated again with the wasp depositing another egg below the entrance.

Typically, many sphecid wasps that nest in pithy stems or borings in wood construct nests containing a linear series of cells. The cells are sealed by partitions that separate siblings, thus preventing cannibalism. Further, nests are normally closed before eggs hatch so that females have no contact with their progeny. Thus, the progressive feeding, maternal attention, and lack of partitions is noteworthy in *K. nordenae*.

Cocoon.—The cocoon also is unique among the Crabroninae. The typical crabronine cocoon is more or less ovoid, circular in cross section, the posterior end tapers rather narrowly, and there is a pore at the anterior end, as in *Ectemnius paucimaculatus* (Packard) (Krombein, 1964). The cocoon of *Krombeinictus* (Fig. 10) is broadly ovoid, tapers very slightly posterad, and lacks a pore at the anterior end. The upper surface is only slightly convex so that in



Figs. 7–11. *Krombeinictus nordenae*. 7, Female, apex of abdomen lateral oblique; note median brush of setae on last tergum. 8, Female, apex of abdomen, lateral oblique from rear; note dried secretion on last segment, and on fifth sternum. 9, Nest diagram. 10, Cocoon in section of internode from which adult emerged. 11, Cocoon in section of internode, oblique; note ample space for passage of adults.

cross section the cocoon is more curved on the side that is appressed against the rounded inner wall of the internode. Cocoon dimensions are 6–9 mm long, 2.6–3.4 mm wide, and 2.0–2.1 mm high.

There is a space at least 2 mm high between its upper surface and the opposite inner wall of the cavity (Fig. 11). A cocoon of this shape permits the mother to crawl over a cocoon to carry a mature larva toward the lower end of the cavity, or for a newly emerged adult from lower in the internode to crawl over a higher cocoon to reach the nest entrance.

Larva.—The data above support our conclusion that the female feeds her larva progressively. We found larvae in various stages of development, but never with any prey or inedible prey fragments such as wings and legs that one would expect to find in the nest of a predaceous wasp. The problem of larval food identity was finally solved when we examined the exuviae of post-defecated larvae, and adjacent fecal wastes. Unmistakably, small grains of pollen had been excreted with the meconium (Fig. 12) which were identical in size and appearance with grains of *Humboldtia* pollen (Fig. 13). Also, we noted that freshly preserved larvae had a distinct yellow color reminiscent of that seen in bee larvae that have fed on pollen. Variations in larval bee color are attributed to pollen color (Norden, 1984).

Later in our investigation, Rickson sent us a female of *K. nordenae* that he collected from an internode in Gilimale. We found clumps of *Humboldtia* pollen grains on the mandibles and hypostomal setae beneath the head (Figs. 14, 15). Due to the oily pollenkitt that envelops the pollen grains, they tend to adhere to each other and to insects that come in contact with the stamens.

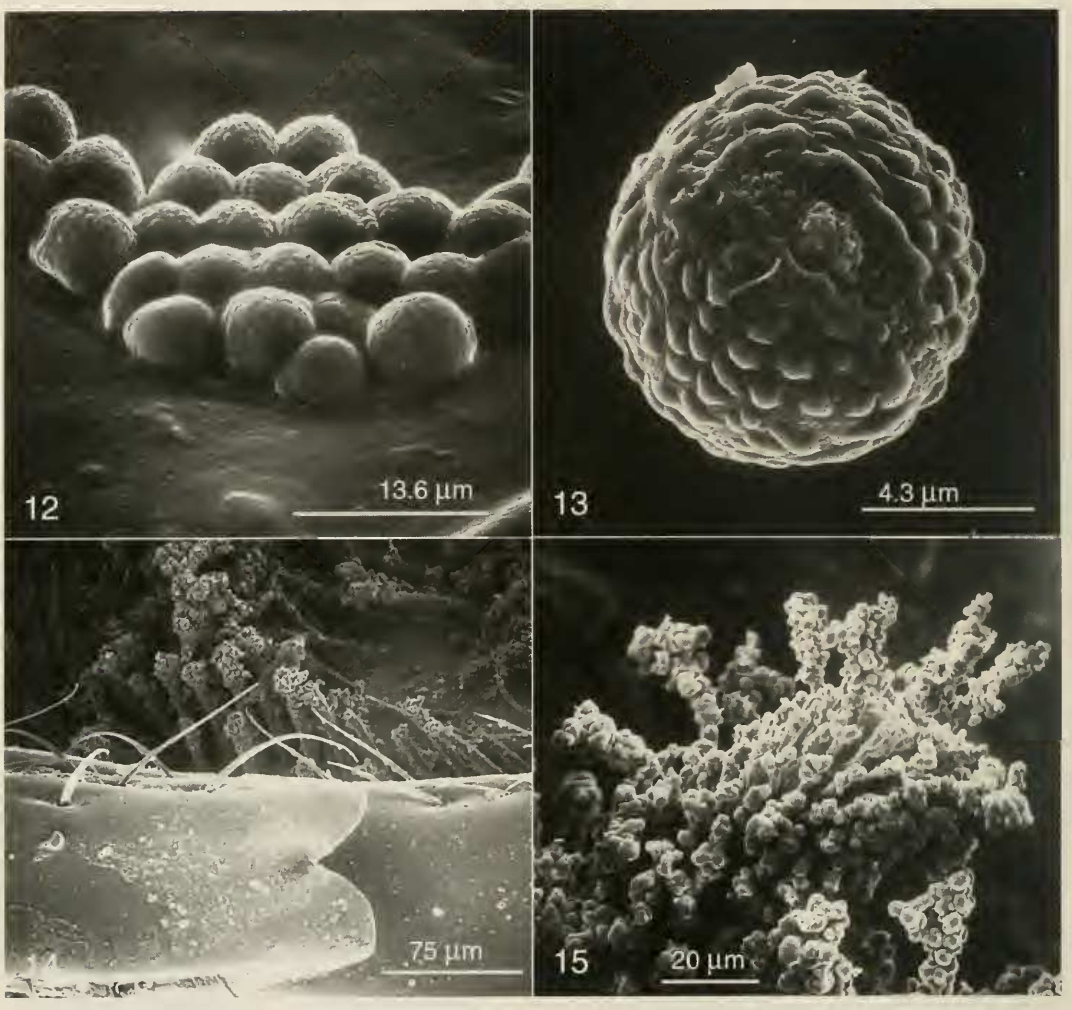
We infer from these data that the female probably gathers a quantity of the clumped *Humboldtia* pollen on the hypostomal area, returns to the internode, and deposits the pollen on the inner wall next to the head of the larva. Again, this feeding behavior is remarkable and in contrast to all known sphecids whose larval food consists of paralyzed arthropods.

Discussion

Behaviorally, *K. nordenae* is unusual or unique among Sphecidae in several characteristics of its life history. The female manifests extraordinary maternal care, rearing one larva at a time, and feeding it progressively. Progressive provisioning has not been noted previously for any Crabroninae. Evans (1966) reported that it developed independently at least four times in the Nyssoninae. Evans also noted that eggs are produced more slowly in progressive provisioners than in mass provisioners. However, the slow development that characterized our nests may actually be related to scarcity of pollen and thus a slower rate of feeding rather than to the rate of egg production. *Humboldtia* flowering occurs throughout the year, but the major production of inflorescences is usually February to June.

The foundress with several brood in varying stages of development forms a subsocial group. Additional field observations are needed to ascertain whether this subsocial group reaches the level of social behavior by having a daughter join the foundress in caring for later brood.

There is also the possibility that *K. nordenae* is so coadapted to *Humboldtia* that the wasp nests only in the plant's internodes, where nearby there is a plenitude of extrafloral nectaries for adult feeding, and pollen when the plant is in bloom. It is noteworthy that the wasp was never collected during the dozen years of the Smithsonian's "Ceylon Insect Project," 1968–1980. None of the project specialists collected on *Humboldtia*, but several of us, including the first author on a number of trips, collected at emergence holes in dead wood, and in tunnels in wood, and failed to find *K. nordenae* in these other plants. If *K. nordenae* is in fact associated only with *Humboldtia*, we wonder if it or other species of *Krombeinictus* may have a similar relation-



Figs. 12–15. *Humboldtia laurifolia* pollen. 12, Pollen mass in meconium within cocoon of *Krombeinictus nordenae*. 13, Grain from flower bud. 14, Pollen grains clumped on hypostomal setae behind mandibular apex of female *K. nordenae*. 15, Pollen grains massed on setae beneath head of female *K. nordenae*.

ship in southern India with *H. decurrens* and *H. brunonis*.

The cocoon also is unlike that of any other known crabronine. Clearly it is an adaptation to the morphology of the internode cavity and nesting behavior of the foundress which permits movement of adults throughout the cavity. The cocoon of the normal twig-nesting crabronine is slightly less in diameter than that of the cavity. The larva spins a loose network of silken guy-lines against the entire wall of the cavity and then constructs the cocoon, suspending it within the network (Krombein, 1964, fig 7b, shows cocoons not in contact with cell wall). The cocoon of *K. nordenae* is spun directly in contact with the rounded inner wall of the internode, and there are only a few silken guy-lines along the cocoon margins.

Finally, and perhaps most significant, the species is extraordinarily different from all other known Sphecidae in feeding its larvae pollen rather than paralyzed arthropod prey.

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